

Abundance, biomass and functional structure of the saprophagous macrofauna in the litter and soil of Mediterranean oak forests

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Summary. The saprophagous macrofauna (macroarthropods, gastropods, earthworms) was sampled in five Mediterranean forests of southern France: two holm oak (*Quercus ilex*) sites on limestone, two downy oak (*Q. pubescens*) sites on limestone and a holm oak site on schist. The total biomass was high, ranging from 52.1 to 113.1 g fresh mass m⁻². Classification of species into functional groups (epigeic, epi-anecic, anecic and endogeic) showed that the four groups were well represented in this region. However, the density and biomass of epigeic macroarthropods (mainly millipedes) were significantly higher at the holm oak sites on limestone (186 ind. m⁻²; 9.6 g m⁻²) than at the other sites. In contrast, the density and biomass of epi-anecic earthworms (*Lumbricus* spp.) were higher at the downy oak sites on limestone (13 ind. m⁻²; 16.7 g m⁻²). Anecic earthworms (*Aporrectodea* and *Scherotheca* spp.) were dominant in terms of biomass at all sites (overall mean 56.6 g m⁻²). Although the results are consistent with possible competitive interactions between epigeic macroarthropods and epi-anecic earthworms, they also show a high degree of coexistence between both of these groups and anecic earthworms. The study provides an insight into the possible responses of the macrofauna of N-W Europe to climate change towards warmer and drier conditions. There is potential for maintenance of all the functional groups that take part in the formation of forest mull.

Key words: Soil macroarthropods, earthworms, functional groups, humus form, Mediterranean forests, climate change

Introduction

Saprophagous macrofauna organisms (macroarthropods, gastropods, earthworms), which are involved in the fragmentation of dead plant material, its incorporation into the soil and mixing with mineral particles, are major regulators of the decomposition process and have considerable effects on the humus form (Bal 1982; Anderson 1988; Schaefer 1991a, b). These animals were long regarded as not very abundant in the Mediterranean climate region of southern Europe, mainly on the basis of Volz's (1962) results obtained in summer. This season is in fact unfavourable for sampling soil macrofauna under Mediterranean conditions (Baker et al. 1992; David 1995). More recent data on the communities of earthworms (Bouché 1978; Cortez 1998) and macroarthropods (Janati-Idrissi 1988; David et al. 1999) have shown that these two groups locally reach high densities and biomasses. In limestone areas, the biomasses of millipedes (Diplopoda) are even the highest ever measured in Europe (David 1995). Howe-

ver, no other study has been undertaken to estimate the size of the whole macrofauna community in a Mediterranean forest soil since that of Volz (1962).

In the present study, the saprophagous macrofauna was sampled in five oak forests of the Languedoc region (southern France) with the following aims:

- 1) To assess the abundance and biomass of all the species occurring at each site and examine the functional structure of the community, i.e. the distribution of biomass among different functional groups.
- 2) At the regional scale, to draw a first comparison between the soil macrofauna of evergreen oak forests dominated by the holm oak, *Quercus ilex* and deciduous oak forests dominated by the downy oak, *Q. pubescens*.
- 3) At the continental scale, to compare the characteristics of the saprophagous macrofauna in Mediterranean forests and humid temperate forests – where data on soil animal communities are available for a number of sites. This can provide an insight into the possible responses of the macrofauna of northwestern Europe to climate change towards warmer and drier conditions.

Materials and Methods

Study sites

The study area extended from about 20 km north of Montpellier to about 45 km west. The climate, though rather humid with a cool winter, is typically Mediterranean because of the period of severe drought occurring every summer. Five oak forests representative of the vegetation and soils of the region were chosen. The vegetation was not described in detail in this study, the main components of the leaf litter being merely sorted on quadrats and weighed (Table 1). Three sites were dominated by holm oak (two on limestone and one on schist) and two sites were dominated by downy oak (both on limestone). The stands were interspersed with small open areas, as is frequently the case in this region, except at the schist site which was very closed. Some characteristics of the soil – soil type according to Duchaufour's (1995) classification, texture and pH of the upper soil layer (0–5 cm), humus form, nature of stones – were obtained from field observations, pedological maps and unpublished material (Table 1).

Sampling procedure

A 900 m² sampling site was identified in each forest. All families of large-sized invertebrates known to feed on litter or faeces of litter-feeders were included in the saprophagous macrofauna (Petersen & Luxton 1982). Macroarthropods and gastropods were sampled in spring (May–June) and autumn (October–November). Fourteen quadrats of 25 × 25 cm were selected at random at each site, excluding outcrops of rock without soil. In each quadrat the litter and top few centimetres of soil were collected from within a metal frame and macroarthropods and gastropods were sorted by hand. The underlying soil layer was checked for the presence of large specimens but was not collected. The surface soil was then taken to the laboratory where the remaining fauna was extracted by Tullgren funnels 25 cm in diameter for 10–14 days. The catch was collected in water and sorted every day. Macroarthropods and gastropods were weighed alive, then preserved in alcohol for subsequent examination.

Earthworms were sampled from late autumn to late winter (November–March), on several occasions at each site, avoiding frost days. Sampling was not undertaken at the same time as for macroarthropods because samples taken in May–June and October at the same sites yielded much lower abundances. 10–12 quadrats of 50 × 50 cm were selected at random in each site. The litter was first collected from within a metal frame and checked for the presence of earthworms. Five litres of 0.2 % formalin were applied on the soil to expel earthworms, and then 5 litres of 0.3 % and 0.4 % solution at 10-minute intervals. Finally, in each quadrat, a 30 × 30 cm area of soil treated with formalin was dug to a depth of at least 20 cm and hand-sorted for earthworms. This made it possible to collect certain species such as *Vignysa popi*, of which no specimen was expelled by formalin. The worms were weighed after preservation in 4 % formalin and blotting.

Identification and functional classification

Adult specimens were identified to species level according to Germain (1930, 1931), Vandel (1960, 1962), Bouché (1972), Demange (1981) and Blower (1985). These authors' nomenclature was updated

Table 1. Location and main characteristics of the five forest sites studied. The abbreviation used for each site in the text is given on the second line of the table

	Holm oak forest on limestone		Downy oak forest on limestone		Holm oak forest on schist
	<i>HOL1</i>	<i>HOL2</i>	<i>DOL1</i>	<i>DOL2</i>	<i>HOS</i>
<i>Location</i> (nearest village)	Le Grand Bois (Puechabon)	Bois de la Rouvière (Montarnaud)	Bois du Patut (Les Camps)	Bois de la Rouvière (La Boissière)	Bois des Moulesses (Vailhan)
<i>Coordinates</i>	43°43'58" N 3°38'38" E	43°39'23" N 3°40'42" E	43°48'16" N 3°49' E	43°39'25" N 3°40'22" E	43°34'11" N 3°18'13" E
<i>Altitude</i>	305 m	275 m	230 m	240–245 m (slope S-W)	190–200 m (steep slope S-E)
<i>Leaf litter components</i> (% dry mass)					
<i>Quercus ilex</i>	95 %	71 %	.	4 %	67 %
<i>Quercus pubescens</i>	+	3 %	99 %	84 %	6 %
<i>Arbutus unedo</i>	+	21 %	.	11 %	17 %
<i>Viburnum tinus</i>	.	.	.	.	8 %
<i>Buxus sempervirens</i>	3 %	+	+	.	.
<i>Parent material</i>	Limestone	Limestone with silex	Limestone	Limestone with silex	Schist
<i>Soil type</i>	fersiallitic red	fersiallitic red	fersiallitic brown	leached fersiallitic	acid brown
Texture	silty clay	silty clay	silty clay	sandy-clayey silt	sandy-clayey silt
pH (H ₂ O)	7.1–7.2	6.9–7.5	7.7	6.2–6.5	5.9–6.0
Humus form	mull	mull	mull	mull	mull (moder locally)
Nature of stones	calcareous	calcareous and siliceous	calcareous	siliceous	siliceous

when necessary. All immature millipedes and woodlice could be assigned to a species using morphological characters. This was also the case for most immature earthworms. When juveniles of similar species were found together at a site (e.g. pigmented species of *Aporrectodea* and *Scherotheca*), an analysis of individual body sizes (number of segments and fresh mass) allowed the species to be separated with a small margin of error. Arionid slugs and elaterid larvae could not be precisely identified and, depending on the species, they may or not feed on leaf litter (Schaefferberg 1942; Jennings & Barkham 1979). There is therefore some uncertainty concerning the saprophagous status of these two taxa in the present study.

Classification of species into ecological categories (epigeic, anecic, endogeic) – defined by Bouché (1972) on the basis of the morphology and distribution in the soil of earthworms – was extended to the other taxa using purely functional criteria (established for some species and presumed for others – David et al. in prep.). The three criteria were the species' share in the processes of fragmentation, incorporation and bioturbation (i.e. fine organomineral mixing). All macroarthropods and gastropods were provisionally considered as epigeic species. This functional group, as defined, is strongly involved in fragmentation of surface litter, incorporates its organic faeces only at a shallow depth (millimetres to centimetres) and participates little in bioturbation. Bouché's (1972) classification was retained for earthworms. However, epi-anecic species (in the genus *Lumbricus*) and anecic species (in the genera *Aporrectodea* and *Scherotheca*) were kept distinct, because the former seem to be much more clearly involved in fragmentation of leaf litter than the latter (Ferrière 1980; Bernier 1998; Jégou et al. 1998).

Data analysis

The mean densities (numbers of individuals m^{-2}) and biomasses (g fresh mass m^{-2}) of invertebrates at each site were compared by analysis of variance (ANOVA). Homogeneity of variances was tested by the $F_{\max}$ -test and, if variances were heterogeneous, data were transformed before ANOVA using either logarithmic or square root transformation (Sokal & Rohlf 1995). The Tukey-Kramer procedure was used for multiple comparisons among pairs of means (Sokal & Rohlf 1995).

Results

At least 23 saprophagous taxa belonging to 12 families were found in the five oak forests studied (Table 2). These included millipedes (Glomeridae, Julidae, Polydesmidae), woodlice (Armadillidae, Armadillidiidae, Philosciidae, Porcellionidae), snails (Pomatidae), earthworms (Hormogastridae, Lumbricidae) and, subject to confirmation of their feeding habits, insect larvae (Elateridae) and slugs (Arionidae). Among macroarthropods, millipedes were the most abundant, accounting for 55–76% of individuals and 64–97% of the biomass according to the site. The dominant species were the glomerid *Glomeris marginata* at sites on limestone and the small julid *Leptoiulus belgicus* on acid soil. Although gastropods were not frequent overall, the operculated snail *Pomatias elegans* reached a substantial biomass (shell included) at one site. Among earthworms, the most abundant species varied according to the site. In terms of biomass, however, all the communities were dominated by an anecic lumbricid species (contributing 47–78% of the earthworm biomass), which was either a giant *Scherotheca* species endemic to the region or *Aporrectodea nocturna*. Locally there were also substantial biomasses of epi-anecic earthworms (*Lumbricus terrestris* in limestone areas and *L. centralis* on acid soil) and endogeic earthworms (the endemic hormogastrid *V. popi* in limestone areas and the lumbricid *Octolasion cyaneum* on acid soil).

ANOVAs revealed highly significant differences among sites in the abundance and biomass of macroarthropods ($F_{4/65} = 16.58$, $P < 0.001$ for the square root of density; $F_{4/65} = 15.96$, $P < 0.001$ for the square root of biomass). Multiple comparisons tests showed that population density was significantly higher at the two holm oak sites on limestone than at the three other sites (Table 2). Likewise, biomass was significantly higher at HOL2 than at DOL1, DOL2 and HOS; it was significantly higher at HOL1 than at DOL2 and HOS.

Gastropods were only found at two downy oak sites on limestone (Table 2). ANOVAs of log-transformed data showed no significant difference between sites, either for density or biomass. The overall means under downy oak were 7 ± 2 individuals m^{-2} for density and 2.6 ± 1.1 g m^{-2} for biomass.

Table 2. „Density and biomass (mean $\pm$ standard error) of the main groups of saprophagous macrofauna in five oak forests of the Languedoc region (HOL1, HOL2, DOL1, DOL2 and HOS described in Table 1). The relative frequency of species is detailed for each group. In each half of the table (data in density and biomass, respectively) means followed by the same letter within a line are not significantly different at $P = 0.05$ by the Tukey-Kramer test

	Density (ind. m ⁻²)					Biomass (g live mass m ⁻²)				
	HOL1	HOL2	DOL1	DOL2	HOS	HOL1	HOL2	DOL1	DOL2	HOS
Macroarthropods:	188 $\pm$ 33^a	184 $\pm$ 25^a	50 $\pm$ 10^b	57 $\pm$ 13^b	43 $\pm$ 14^b	8.0 $\pm$ 1.2^{ab}	11.2 $\pm$ 2.4^a	4.2 $\pm$ 0.9^{bc}	3.4 $\pm$ 1.1^{cd}	0.3 $\pm$ 0.1^d
<i>Glomeris marginata</i>	56 %	59 %	50 %	24 %	—	73 %	80 %	72 %	73 %	—
<i>Glomeridella kervillei</i>	—	—	—	—	5 %	—	—	—	—	4 %
<i>Cylindroiulus caeruleocinctus</i>	20 %	12 %	5 %	3 %	—	24 %	9 %	3 %	9 %	—
<i>Leptoiulus belgicus</i>	—	2 %	—	—	69 %	—	1 %	—	—	60 %
<i>Polydesmus angustus</i>	—	—	—	36 %	—	—	—	—	1 %	—
<i>Porcellio gallicus</i>	4 %	2 %	20 %	4 %	7 %	2 %	—	7 %	5 %	18 %
<i>Armadillidium vulgare</i>	1 %	4 %	16 %	2 %	—	—	5 %	6 %	—	—
<i>Armadillo officinalis</i>	—	2 %	7 %	2 %	—	—	3 %	13 %	8 %	—
<i>Philoscia affinis</i>	—	2 %	—	—	—	—	1 %	—	—	—
<i>Elaterid larvae</i>	19 %	16 %	2 %	28 %	19 %	1 %	1 %	—	4 %	18 %
Gastropods:	—	—	10 $\pm$ 4^a	3 $\pm$ 2^a	—	—	—	4.7 $\pm$ 2.0^a	0.5 $\pm$ 0.3^a	—
<i>Pomatias elegans</i>	—	—	100 %	—	—	—	—	100 %	—	—
<i>Arion sp.</i>	—	—	—	100 %	—	—	—	—	100 %	—
Epianecic earthworms:	—	1 $\pm$ 1^c	21 $\pm$ 4^a	7 $\pm$ 2^b	6 $\pm$ 2^b	—	1.7 $\pm$ 1.4^b	20.2 $\pm$ 6.6^a	13.9 $\pm$ 4.4^a	7.5 $\pm$ 3.0^{ab}
<i>Lumbricus terrestris</i>	—	100 %	100 %	100 %	—	—	100 %	100 %	100 %	—
<i>L. centralis</i>	—	—	—	—	100 %	—	—	—	—	100 %
Anecic earthworms:	17 $\pm$ 4^{bc}	21 $\pm$ 3^{ab}	35 $\pm$ 4^a	13 $\pm$ 2^{bc}	7 $\pm$ 2^c	33.0 $\pm$ 6.6^a	45.4 $\pm$ 13.6^a	41.5 $\pm$ 8.5^a	93.7 $\pm$ 22.9^a	66.8 $\pm$ 36.0^a
<i>Scherotheca monspessulensis</i>	10 %	20 %	—	63 %	—	23 %	64 %	—	91 %	—
<i>S. gigas orbiensis</i>	—	—	—	—	100 %	—	—	—	—	100 %
<i>Aporrectodea nocturna</i>	90 %	57 %	100 %	27 %	—	77 %	31 %	100 %	8 %	—
<i>A. caliginosa meridionalis</i>	—	23 %	—	10 %	—	—	5 %	—	1 %	—
Endogeic earthworms:	13 $\pm$ 4^a	6 $\pm$ 3^a	20 $\pm$ 7^a	3 $\pm$ 1^a	25 $\pm$ 8^a	11.1 $\pm$ 3.5^{abc}	1.5 $\pm$ 0.8^c	27.1 $\pm$ 12.6^{ab}	1.6 $\pm$ 0.6^{bc}	15.1 $\pm$ 4.0^a
<i>Octolasion cyaneum</i>	43 %	12 %	8 %	31 %	74 %	27 %	35 %	3 %	66 %	86 %
<i>Allolobophora chlorotica</i>	—	—	10 %	—	—	—	—	2 %	—	—
<i>Aporrectodea rosea</i>	49 %	65 %	—	58 %	26 %	45 %	40 %	—	29 %	14 %
<i>A. caliginosa caliginosa</i>	—	23 %	—	11 %	—	—	25 %	—	5 %	—
<i>Vignysa popi</i>	8 %	—	82 %	—	—	28 %	—	95 %	—	—

As regards earthworms, the greatest differences among sites concerned epi-anecic *Lumbricus* species. No specimen was found at HOL1 and, for the other sites, ANOVAs of log-transformed data revealed significant differences in abundance ($F_{3/40} = 14.74$, $P < 0.001$) and biomass ($F_{3/40} = 5.47$, $P < 0.01$). Multiple comparisons of means showed that the density was significantly lower at HOL2 than at the three other sites – the highest figures being recorded at the downy oak sites on limestone (Table 2). Likewise, biomass was significantly lower at HOL2 than at the downy oak sites on limestone – the site on schist having an intermediate biomass.

The abundance of anecic earthworms differed significantly among sites ($F_{4/50} = 8.22$, $P < 0.001$ for log-transformed data), but not their biomass. The reason for this was twofold: firstly, the site with the highest density (DOL1) did not have giant worms (*Scherotheca*) but only *A. nocturna*, which balanced the mean biomasses; and secondly, the horizontal distribution in terms of biomass was very aggregative where *Scherotheca* species were present, which made it impossible to obtain significant differences among sites. The mean biomass of anecic earthworms in the five oak forests was $56.6 \pm 9.2 \text{ g m}^{-2}$.

The abundance of the endogeic species was minimal at two neighbouring sites (HOL2 and DOL2, both on limestone with flints). However, ANOVAs of log-transformed data revealed significant differences among sites only in biomass ($F_{4/50} = 4.81$, $P < 0.01$). Multiple comparison tests showed that biomass was significantly lower at HOL2 than at DOL1 and HOS, and significantly lower at DOL2 than at HOS.

The main differences in the functional structure of communities, on the basis of biomass data, are summarized in Fig. 1. Although all the communities studied were dominated by anecic earthworms, they could be divided into (1) the communities of holm oak sites on limestone, characterized by a large proportion of epigeic macroarthropods (accounting for 17% of the total biomass) and very few epi-anecic earthworms; (2) the communities of downy oak sites on limestone, with a lower proportion of epigeic species (macroarthropods plus gastropods) and many more epi-anecic earthworms than the preceding sites (accounting for 16% of the total biomass); and (3) the community of the holm oak site on schist, characterized by an insignificant epigeic macrofauna and a proportion of epi-anecic earthworms midway between the two preceding cases.

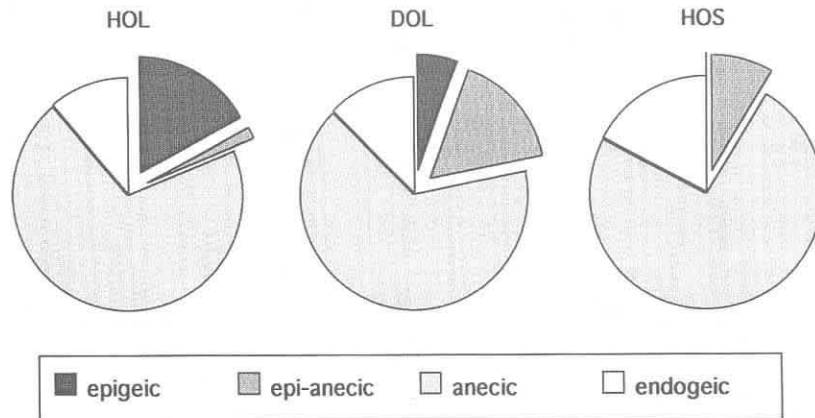


Fig. 1. Relative biomass of the functional groups of saprophagous macrofauna (epigeic, epi-anecic, anecic and endogeic) in three types of Mediterranean forests: holm oak on limestone (HOL), downy oak on limestone (DOL) and holm oak on schist (HOS)

Discussion

The biomass of saprophagous macrofauna proved to be high in the Mediterranean oak forests of southern France. In this study, figures ranging from 52.1 to 113.1 g fresh mass m⁻² were recorded at a variety of sites in terms of vegetation and parent material. Even in the forest on schist, where there was a large turnover of species in comparison with the forests on limestone, biomass was considerable. The occurrence of a markedly dry season therefore does not appear to hinder the existence of soil macrofauna communities. The contrast with Volz's (1962) results perhaps emphasizes more the need to sample at appropriate seasons (spring-autumn for macroarthropods, winter for earthworms) than real differences between sites.

Key-functions for the cycling of organic material and formation of the humus profile – i.e. fragmentation of litter by epigeic plus epi-anecic species, incorporation of organic matter deep into the soil profile by epi-anecic plus anecic species and fine organomineral mixing by epi-anecic, anecic and endogeic species – were ensured at all the sites studied. As a result, the humus forms were all of mull type, with a thin litter layer directly overlying organomineral aggregates. Although species richness was low at some sites (e.g. only eight species at HOS and ten at HOL1), it should be noted that each of the three functions (fragmentation, incorporation, bioturbation) was performed by several species at each site, which may confer some functional stability to the communities (Belotti & Babel 1993).

The present study suggests that, in the *garrigues* on limestone of the Languedoc region, there are more *L. terrestris* and gastropods under downy oak (*Q. pubescens*) and more macroarthropods (mainly represented by *G. marginata*) under holm oak (*Q. ilex*). Subject to subsequent confirmation, fragmentation of the leaf litter could therefore be ensured by different taxa under evergreen and deciduous oaks. As the phenology of litter fall is not the same for the two oak species and the periods of activity of *L. terrestris* and *G. marginata* only partially overlap, the decomposition dynamics may be very different in the two types of Mediterranean forests.

The unusually high biomass of saprophagous macroarthropods, especially millipedes, at holm oak sites on limestone confirms previous results (Janati-Idrissi 1988; David 1995) and should be emphasized. This demonstrates that the epigeic fauna can reach peak biomasses in the presence of a substantial biomass of anecic earthworms. The assumption that anecic earthworms tend to exclude the epigeic macrofauna from mull soils due to inter-specific competition for food (Bouché 1978; Kime 1990), should be reconsidered by making a distinction between epi-anecic and anecic species. Although the data from the Mediterranean sites are consistent with possible competitive interactions between epigeic macroarthropods and epi-anecic *Lumbricus* species, they also show a high degree of coexistence between these two groups and anecic earthworms (in the restricted sense *A. nocturna*, *A. caliginosa meridionalis*, *S. monspessulensis* and *S. gigas orbiensis*). This could be explained by a much lower rate of leaf litter consumption than is generally assumed for anecic earthworms. Zachariae (1965) observed that certain anecic species fed preferentially on faeces of other saprophagous animals — as do endogeic earthworms (Scheu & Sprengel 1989; Bonkowski et al. 1998) — and only subsequently on leaf litter. This is in keeping with the gut content analyses made by Ferrière (1980) and Bernier (1998). It can be suggested that the anecic group is more in cooperation than in competition with the epigeic and epi-anecic groups. More detailed studies are however needed on this topic, particularly on the trophic behaviour of *Scherotheca* species.

A comparison between soil macrofauna communities from Mediterranean and humid temperate forests (Schaefer 1991a) shows two distinct differences: (1) Purely epigeic earthworms are virtually absent from Mediterranean forest soils. They can however be replaced by other epigeic animals, mainly macroarthropods, which ensure the fragmentation of surface litter. The latter could even be increased, insofar as the annual rate of litter consumption is about twice as high in macroarthropods (9–11 g dry mass g⁻¹ live mass year⁻¹ – Van der Drift 1975; David 1987) as in litter-feeding earthworms (5–6 g dry mass g⁻¹ live mass year⁻¹ – Satchell 1983). (2) In the Mediterranean region, anecic and epi-anecic earthworms are more active in winter, when the soil is moist, as is shown by the quasi-absence of response to formalin from

mid-May to mid-November. They nevertheless have considerable effects on the soil, considering the amount of casts visible at the surface throughout the year.

The comparison between the two climatic areas does not support the view that an increase in temperature is likely to modify the functional structure of earthworm communities towards a relative increase of endogeic populations (Lavelle et al. 1997). The proportion of endogeic biomass – whether in the total macrofauna biomass or the earthworm biomass – is not larger in the Mediterranean sites than in mull sites of N-W Europe, despite mean annual temperatures higher by 5–8 °C. The largest proportion of endogeic earthworms in this study (28 % of the total biomass and 31 % of the earthworm biomass at DOL1) is of the same order of magnitude as in mull soils of Germany and Belgium (Schaefer 1990; David et al. 1993), and is much smaller than in a northern woodland in Sweden, where endogeic earthworms accounted for 73 % of the total biomass and 77 % of the earthworm biomass (Axelsson et al. 1984).

It can be concluded that, in the hypothesis of an increase in temperature with drier summers in N-W Europe, all the functional groups of saprophagous macrofauna can be preserved where permitted by soil conditions – including the epigeic group if macroarthropods and gastropods are taken into account. The migration or introduction of species from warmer and drier areas would not necessarily be required, as certain species which are abundant under a Mediterranean climate are already widespread at higher latitudes in Europe (e.g. the epigeic *G. marginata* and *P. elegans*, the epi-anecic *L. terrestris* and *L. centralis*, the anecic *A. nocturna*, and the endogeic *O. cyaneum* and *A. rosea*). The proportions of functional groups might change more markedly in Mediterranean forest soils if they became more arid; however, concerning this point, there are few data for comparison.

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